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Spectral Sensitivity of Vision in the Mantis Shrimp, *Gonodactylus oerstedii*, Determined Using Noninvasive Optical Techniques

THOMAS W. CRONIN AND CHRISTINA A. KING*

Department of Biological Sciences, University of Maryland Baltimore County, Catonsville, Maryland 21228

Abstract. Compound eyes of stomatopod crustaceans have many unique design features. Recently developed intracellular optical physiology techniques permit the measurement of spectral sensitivity functions in intact eyes of these animals. We tested four technically distinct approaches to measurement of spectral sensitivity in peripheral ommatidia of the compound eyes of *Gonodactylus oerstedii*. Each technique was evaluated for (1) the time required to measure a complete sensitivity spectrum, (2) reproducibility of results, and (3) suitability for use in a fully automated system. A spectral scan technique, in which the visual response is held constant by varying stimulation intensity throughout the scan, was found to be superior. With it, a complete, highly reproducible measurement of spectral sensitivity from 400 to 650 nm at 10-nm intervals could be accomplished automatically within 20 min. The photoreceptors were maximally sensitive near 540 nm, and the sensitivity curve was well described by the absorptance curve for a retinal$_1$-based visual pigment with peak absorbance at 537 nm and peak density equal to 0.5 OD.

Introduction

The compound eyes of stomatopod crustaceans are among the most unusual visual organs ever evolved, and several laboratories have recently taken up their investigation. These new studies confirm Exner's (1891) original observation that vision in these animals is triple; as many as three sets of ommatidia in a single compound eye may view the same spatial region (Horridge, 1978; Schiff *et al.*, 1985, 1986a, b; Cronin, 1986; Schiff and Candone, 1986). Each eye is divided by a central band of 2 to 6 ommatidial rows; patches of ommatidia on each side of this band share fields of view with it.

The triple design is conserved among three of the four stomatopod superfamilies (Manning *et al.*, 1984), and offers unique opportunities for color vision. For instance, in the gonodactyloid stomatopods, where the central band includes six ommatidial rows, each is of special design (Marshall, 1988). Colored filters, which must affect the spectral sensitivities of the underlying photoreceptors, are found in some of these rows. Thus, the various rows, as well as ommatidia outside the central band, may vary in spectral sensitivity; and as they simultaneously view an object its color may be analyzed (Marshall, 1988). Gonodactyloid stomatopods frequently live in shallow, well-lit habitats, and are marked with striking, species-specific colors (Caldwell and Dingle, 1975), so color vision should be not only possible, but useful.

Learning how stomatopod visual systems respond to pigmentary colors requires the measurement of spectral sensitivity in the various rows of the central band as well as in the more peripheral regions of the eye. Recently, we developed a noninvasive, optical approach to studying crustacean ocular physiology (Cronin, 1989) that is based on intracellular optical physiological techniques developed to study insect vision (*e.g.*, Franceschini, 1975; Stavenga and Kuiper, 1977; Bernard and Stavenga, 1979; Bernard and Wehner, 1980). Measurements are made of changes in reflectance that occur within the deep pseudopupil (Stavenga, 1979) of a selected region of the compound eye as it adapts to light or dark. These changes are caused, at least in insects, by the light-mediated translocation of granules of retinular cell screening pigment to the region of the rhabdom, where

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they reduce the light flux within the photoreceptor (see review of Stavenga, 1979).

Crustacean retinular cells also contain mobile pigment granules (Ludolph *et al.*, 1973; Schönenberger, 1977; Stowe, 1980), which probably bring about the intracellular optical response in their eyes (see also Cronin, 1989). However, in some insects, secondary pigment cells also may respond to light stimuli, which may confound measurements of photoreceptor cell spectral sensitivities (Hamdorf *et al.*, 1986; Land, 1987). Although the secondary response appears to occur only in superposition compound eyes, the use of the technique must be rigorously justified when it is applied to new species.

Optical techniques offer the advantages of (1) knowing precisely what ommatidial region is responding in an experiment and (2) being able to use the same eye repeatedly, so that a variety of regions can be examined. However, because the intracellular optical response is slow relative to electrophysiological responses, the time required for spectral sensitivity measurements can be lengthy. Recently, new approaches and automation have greatly increased the speed and resolution of electrophysiological measurement of spectral sensitivity (Gribakin, 1981; Franceschini, 1984; Menzel *et al.*, 1986; Paul *et al.*, 1986; Steiner *et al.*, 1987). It seemed likely that optical measurements of spectral sensitivity could similarly be improved.

Therefore, we surveyed a variety of methods of measuring spectral sensitivity in a single region of the compound eye of a gonodactyloid stomatopod, *Gonodactylus oerstedii*, using the intracellular optical approach. The selected region (the deep pseudopupil of ommatidia in the dorsomedial region of the eye) probably has only one spectral mechanism operating between 400 and 700 nm (Cronin, 1989), making it relatively easy to compare the results of each approach. The study has led to the development of a spectral scan technique permitting the measurement of a sensitivity spectrum within 20 min.

Materials and Methods

All animals were collected in the Florida Keys and shipped to Maryland for study. A detailed description of the intracellular optical physiological technique, as applied to *G. oerstedii*, is given in Cronin (1989). Here follows a brief description.

Animals were attached dorsal side down to an adjustable, submersible stage using Scutan dental plastic; their eyes were immobilized using the same material. The animal was covered with artificial seawater and adjusted so that all three pseudopupils of the ventral part of one eye were visible. Prior to each experiment, the experimental mantis shrimp was dark-adapted for at least several hours, and commonly overnight.

The deep pseudopupil of the dorsomedial region of a selected eye was centered in the field of view of an incident-light, photometric microscope. Two beams of light were brought into the incident-light path on the same axis, passed through a Zeiss 25-mm Luminar objective protected with an angled, submersible diptube, and entered the eye. One of these, the measuring beam, contained long-wavelength light (>720 nm; Schott RG720 longpass filter) and remained illuminated throughout the experiment. A portion of this beam returned to the photometric microscope after being reflected and/or scattered by material within the deep pseudopupil. The intensity of the returning light alters with dark or light adaptation; these changes provide the signal for measuring visual responses (Cronin, 1989). This intensity was measured with a photomultiplier (Hamamatsu R928) connected via a PARC 1140C quantum photometer to the A/D interface of a microcomputer. Light arriving at the photomultiplier passed through a 720-nm longpass filter, which permitted passage of the measuring beam alone. In these experiments, the measured area of the eye was restricted to about 10 ommatidia by an adjustable rectangular diaphragm mounted in the microscope's upper image plane.

The other beam, the stimulating beam, reached the eye only during the course of a stimulation. Its plane of polarization was set parallel to the line connecting the three pseudopupils of the eye under study, while its wavelength, intensity, and duration could be controlled with the assistance of the microcomputer. Wavelength was altered using an Oriel model 7240 grating monochromator, intensity was adjusted with counterrotating 10-cm diameter quartz neutral density wedges (total density range, 0–3.8), and exposure duration was set using a Uniblitz electromagnetic shutter. The stimulating beam was produced by a Xenon arc lamp, either 75 W or 150 W; its quantal irradiance at each test wavelength was measured daily using a calibrated United Detector Technology PIN-10DP/SB photodiode at the position of the experimental eye. The way in which the stimulating beam was presented varied with each of the experimental approaches, as described below.

Criterion technique

Here, we determined the intensity of light required at each wavelength to elicit a criterion response. Wavelengths were tested every 20 nm from 400 to 660 nm, presented in random order. The response was taken as the average reflectance level during the final 2 s of a 10-s stimulus (see Fig. 1), compared to the average level of reflectance in the dark. The criterion response level was set at 2 to 3%, depending on the responsiveness of the eye under study. Stimulations occurred at 1.5-min inter-

vals. To correct for possible drifts in sensitivity during an experiment, all sensitivities were compared to that at 500 nm, and the 500-nm standard sensitivity was measured frequently throughout each run.

Interpolation technique

Ten-second stimulations were provided at single wavelengths at 1.5-min intervals at various intensities. Responses were quantified as in the criterion experiment, and the experimenter selected intensities expected to produce responses of about 1%, 2%, 4%, and 8%. Data were plotted as percent response *versus* log quantal intensity, and the intensity required for a standard response of 5% was determined from a linear regression line fitted to the points. As in the criterion experiments, sensitivities were compared to that at 500 nm, which was frequently redetermined. Wavelengths at 10-nm intervals from 400 to 640 nm were presented in random order.

Ramp technique

In these experiments, eyes of experimental animals were given a slowly increasing stimulation intensity at each wavelength, and the intensity required for a criterion response was determined by interpolation. The neutral density wedges were set so that the initial stimulation occurred at a level where no response was measureable. Responses were averaged into bins 2 s in length. Each stimulation sequence began with a 20-s dark period. The shutter opened and measurement continued for 10 s longer. The neutral density wedges were then rotated stepwise to decreasing densities, with each step (a density change of about −0.03) following a 2-s measurement period. The intensity continued to increase until the reflectance was 5% above the level measured during the initial 20-s dark period, at which time the shutter closed and the wedges rewound to their initial positions. Subsequent ramps were presented after a 2.5-min dark period. The response curve was smoothed by averaging over three adjacent bins, and the intensity required for a 4% response level was computed from the smoothed curve. As for criterion and interpolation techniques, measured sensitivities were compared to that at 500 nm, which was frequently redetermined. Other wavelengths were presented in random order.

Scan technique

In these experiments, a negative-feedback cycle kept the response "clamped" at a particular level; stimulation intensity was varied at each successive wavelength to maintain the constant response level. Scans began with a 50-s dark period for measurement of the dark-adapted reflectance level. The stimulation wavelength was then set to 400 nm, the intensity set to a level previously determined to produce a response of about 10%, and the animal was exposed to light for 20 min to attain a stable light-adapted reflectance level. A 50-s measurement of this reference reflectance level was then taken. The wavelength was then changed to a new value; in an ascending scan this would be 410 nm, while in a descending scan it would be 650 nm. Measurements were taken in 5-s bins. The average reflectance in each bin was compared to the light-adapted reference reflectance. If the two values did not match to within 0.25%, the density wedges were rotated so as to drive the response towards the desired reference. Thus, if reflectance exceeded the reference level, the density was increased (reducing stimulation intensity), and *vice versa*. Once the match occurred, the current wavelength and quantal intensity were stored, and the monochromator was set to the next wavelength, 10 nm above (ascending scan) or below (descending scan) the current wavelength. Ascending scans continued to 650 nm, and descending scans to 410 nm. When successive scans were taken, the reference level to 400-nm stimulation was once again measured without an intervening stabilization period. Successive scans occurred in opposite directions.

Results

The properties of the intracellular optical responses of *Gonodactylus oerstedii* have been described (Cronin, 1989). Typical responses of a fully dark-adapted eye at two stimulation intensities are illustrated in Figure 1. The eye remained in the dark (only the measuring beam was illuminated) until 0 s, when stimulation commenced. Reflectance from the deep pseudopupil rose to a new steady state in 5 to 10 s. Above threshold and below saturation, the response increased monotonically with quantal intensity. When the stimulation ceased, the reflectance level returned to the dark-adapted baseline in 5 to 10 s. The response levels were computed by comparing the average level in the final 2 s of the stimulation interval with the levels before the stimulus commenced (2-s interval before 0) and during the final 2 s of the post-stimulation period. In Figure 1, these responses were 28.4% (upper trace) and 3.65% (lower trace).

Criterion experiments

The criterion level was set at 2% or 3%, which is far below the maximum response of 25 to 40%. Spectral sensitivity was derived by determining the sensitivity (the inverse of the photon flux) at each test wavelength relative to that at the standard wavelength (500 nm). Each resulting function was normalized to its respective peak, and the overall average curve and standard errors were

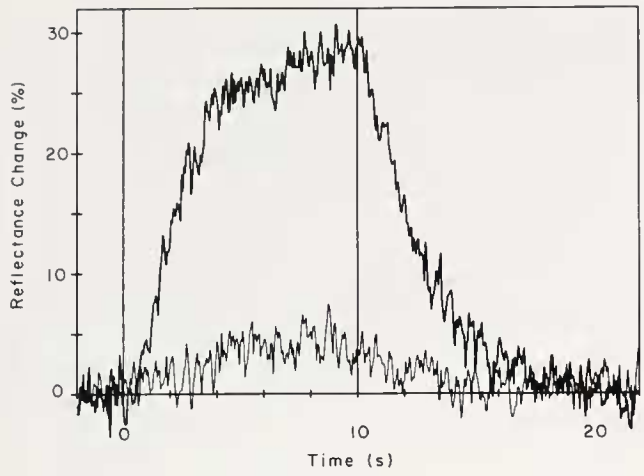

Figure 1. Typical intraocular optical responses, as changes in reflectance, in the deep pseudopupil of the medial ocular region of a compound eye of *Gonodactylus oerstedii*. Stimulation commenced at 0 s (1st vertical line) and ended 10 s later (2nd vertical line). The measuring beam, which was illuminated throughout the experiment, contained wavelengths >720 nm; light of this composition sensitizes the response (see Cronin, 1989). Quantal stimulation intensities were 1.79×10^{13} photons cm^{-2} s^{-1} (upper, dark trace) or 5.61×10^{10} photons cm^{-2} s^{-1} (lower, light trace), which caused responses of 28.4% and 3.65%, respectively.

computed. These were normalized to the peak of the average curve. The resulting function (Fig. 2) peaks at 520 nm, falls away steeply at longer wavelengths and less steeply at shorter wavelengths, and resembles a rhodopsin absorption spectrum. Finding the precise intensity for a criterion response often required several stimuli, so about 3 h were required to measure a single function. The other experimental approaches were designed both to reduce this time and to automate the procedure as much as possible.

Interpolation experiments

In these, the response to an initial stimulation was noted, and subsequent stimulation intensities were selected to produce responses ranging from 1 to 8%. Since the response was compared to both the initial and final dark-adapted levels, two values were obtained at each intensity. Regression lines were computed from the eight resulting points; typical response *versus* log intensity curves are plotted in Figure 3A. The photon flux required for a 5% response at each wavelength was compared to that required for an equivalent response at 500 nm, and sensitivity functions were computed as in the criterion experiments. The average curve for three such experiments (Fig. 3B) has a maximum at 530 nm, and its shape is similar to the function of Figure 2. An entire spectral-sensitivity determination (10-nm intervals, 400–640 nm) required some 3 to 5 h, which was somewhat longer that the time taken for a criterion run. However, more wavelengths were sampled in the interpolation experiments; both methods required similar times for the measurement of each single point.

Ramp experiments

Here we automated the collection of sensitivity spectra. Each stimulation sequence began at a subthreshold intensity and continued until a 5% response was reached. The entire run was executed under computer control, following a list of test wavelengths. A sample response is given in Figure 4A. The eye remained in the dark until the shutter opened at the time indicated by the vertical line, and the neutral density wedges began to step toward lower densities at the time indicated by the arrow. Steps occurred at 2-s intervals. The response curve (solid line) was smoothed by taking a running three-point average (the first and final points were not averaged). In each presentation, the intensity at which the smoothed curve crossed the 4% response level (the horizontal line on the graph) was determined, and sensitivity curves were computed as in the previous sections. The average curve (5 experiments, Fig. 4B) resembles the previous results (Figs. 2, 3B), but contains fewer points. Each run required some 2 h. Furthermore, if animals cleaned their eyes or waved appendages into the measuring beam, large signal fluctuations resulted that disturbed the ramp and frequently aborted measurements. In contrast, in the manual techniques the experimenter easily recognized such artifacts and excluded them from further consideration.

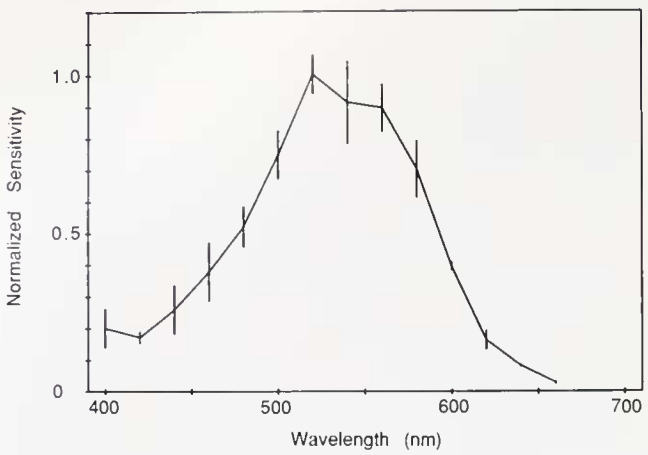

Figure 2. Criterion technique. The curve is the average of four determinations of spectral sensitivity, as described in the text. The vertical lines at each plotted point are the standard errors of the mean.

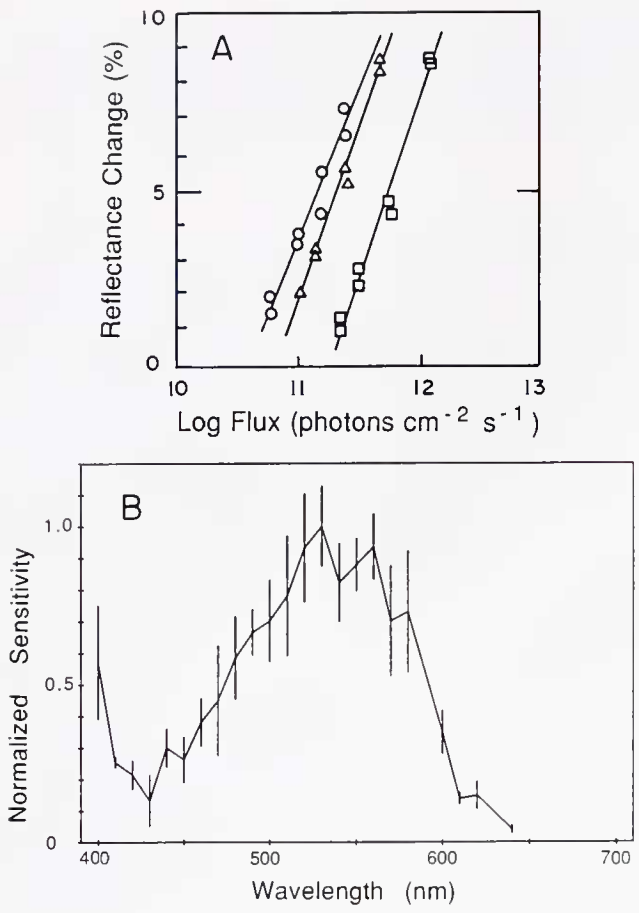

Figure 3. Interpolation technique. A. Response vs. log intensity functions at 3 wavelengths: 550 nm (circles), 500 nm (triangles), and 450 nm (squares). Each set of points is fit with a linear regression function, and the intensity necessary for a 5% response is determined from this. B. Average sensitivity measured by this technique. The curve is the average of three runs; vertical lines are standard errors of the mean.

Spectral scan experiments

This technique was inspired by electrophysiological measurements made by Franceschini (1984) and by Menzel *et al.* (1986). The underlying principle is to "light clamp" the response to any desired level by adjusting stimulation intensity. In our experiments, each measurement was taken over a 5-s interval, approximately one time constant for a typical intracellular optical response. The computer then decided whether to accept the response level or to alter the stimulation intensity and repeat the measurement. As successive measurements occur at wavelengths separated by only 10 nm, relatively little adjustment is required over most of the sensitivity band. Furthermore, any artifacts caused by animal movements are very unlikely to produce signals near the reference level, and so are automatically rejected. The reference level of the response was generally near 10%, somewhat higher than in the previous experiments. This level was chosen to allow the measurement of both negative and positive changes, and to provide some headroom for drift which might occur during a single scan.

The data of an ascending spectral scan, in which the reflectance level was clamped 12.9% above that measured in the unstimulated condition, are plotted in Figure 5A. Each time wavelength increased, a spike appeared in the record, which was subsequently eliminated as the scanning program brought the response to within 0.25% of the reference level. While the form of the record depends to some extent on the spectral distribution of the stimulating beam, at times when sensitivity is increasing

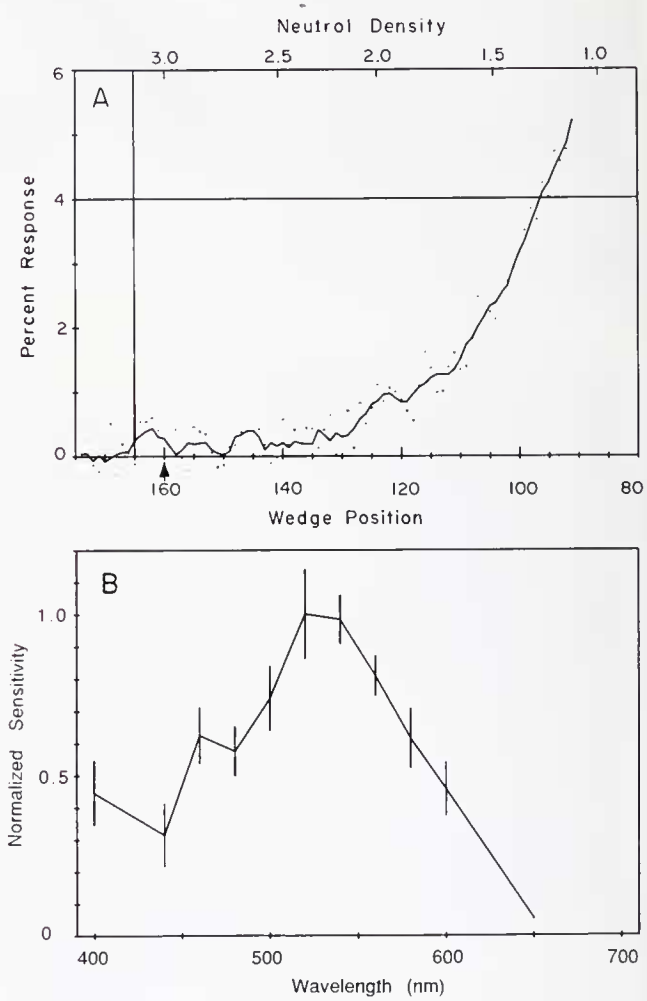

Figure 4. Ramp technique. A. Results of a single measurement (500 nm, reference intensity of 5.68×10^{12} photons cm^{-2} s^{-1}). The eye was initially in the dark (measuring beam only). The shutter opened at the time indicated by the vertical line, when the neutral density wedges were at position 160. At the time indicated by the arrow, the wedges began to rotate to positions of decreased density, with steps (density loss of 0.03/step) occurring at 2-s intervals. When the response reached 5%, the exposure ended. B. Average results of five experiments. Vertical lines indicate standard errors of the mean.

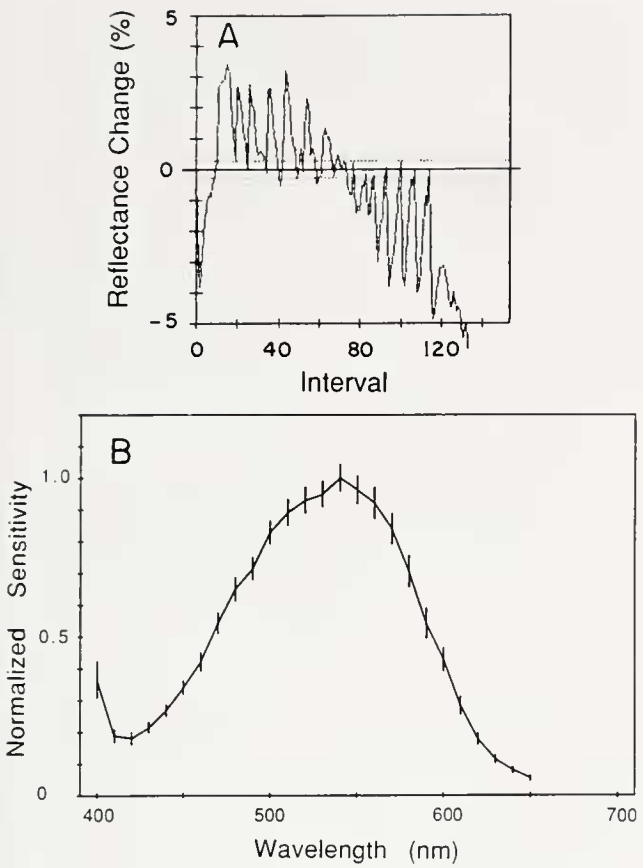

Figure 5. Scan technique. A. Results of a single ascending spectral scan. The scan began at 400 nm at interval 0, and each interval lasted 5 s. Whenever reflectance fell within 0.25% (dotted lines) of the reference level (0% reflectance change), the wavelength and photon flux was recorded and the wavelength was driven to a value 10 nm greater. Whenever the reflectance differed from the reference by more than 0.25%, the density wedges were rotated to alter the stimulation intensity and move the response towards the reference level. In general, each spike in the record occurred as a new wavelength was reached and the negative-feedback loop restored the reflectance to the reference level. The scan ended when the wavelength reached 650 nm. B. Average results of 21 scans in 16 experiments. Vertical lines indicate standard errors of the mean.

successive spikes tend to point upwards, as in the earlier part of the record. As the peak sensitivity is passed, the spikes begin to point downwards, so stimulus intensity must be increased to bring the response back to the reference level. In the illustrated scan, the longest wavelengths contained insufficient light to bring the response to the reference level, and the trace trailed off to decreasing levels of reflectance.

Sensitivity curves were analyzed and averaged as before. The average curve and associated errors for 21 separate scans, taken from 16 individual presentations (some included multiple scans), are plotted in Figure 5B. Scans typically were completed within 15 to 25 min, once the initial 20-min stabilization period was passed (the scan of Fig. 5A required 20 min, 19 s). Thus, starting with a fully dark-adapted eye, four complete scans (2 ascending and 2 descending) could be completed in 2 h or less. Though collecting the data of Figure 5B required a similar amount of time as data collection for the earlier figures, the resulting curve is smoother, and the errors smaller, than in any of the previous data sets. Individual scans tend to be less variable than the separate data sets of the other techniques as well. At moderate levels, response is nearly a linear function of log intensity (Fig. 3A), so the increased precision is unlikely to be due only to the somewhat higher levels of response chosen here.

Discussion

The primary purpose of this study was to develop a rapid and accurate method of measuring spectral sensitivity in particular regions of stomatopod compound eyes. This is an important goal, since the stomatopods may have the most complex visual systems, in terms of peripheral design, in existence; the design is particularly well-suited for color vision (Marshall, 1988).

If color vision exists in stomatopods, it would depend on two unique features of the compound eyes. The first is the multiple overlap of receptive fields of different ommatidia, resulting both from the triple redundancy of the central band and more peripheral retinal regions (Exner, 1891; Horridge, 1978; Schiff *et al.*, 1985, 1986a, b; Cronin, 1986; Schiff and Candone, 1986), and from the complete sharing of receptive fields by the six ommatidial rows in any column of the central band (Horridge, 1978; Marshall, 1988). Second, ommatidia in two of the individual rows of the central band of gonodactyloid stomatopods contain intrarhabdomal colored filters at two separate levels. Like the oil droplets in retinal cones of reptiles and birds, these filters would shift and narrow the spectral sensitivity functions of the photoreceptors lying under them (Hardie, 1988; Marshall, 1988). Therefore, even with a single visual pigment in all rhabdoms, as is the case with *Squilla empusa* (Cronin, 1985), multiple spectral sensitivity functions are expected and the visual field overlaps would permit hue discrimination to occur. In fact, recent unpublished work suggests that many visual pigments exist in the retinas of gonodactyloid stomatopods.

The argument presented in the previous paragraph strictly applies only to the main rhabdom, formed by the fused rhabdomeres of retinular cells 1–7. Crustaceans generally have a single visual pigment, of peak absorption near 500 nm, in the main rhabdoms of all ommatidia and a second one, absorbing at considerably shorter wavelengths, in the overlying rhabdomere of the 8th retinular cell (Cummins and Goldsmith, 1981; Martin and

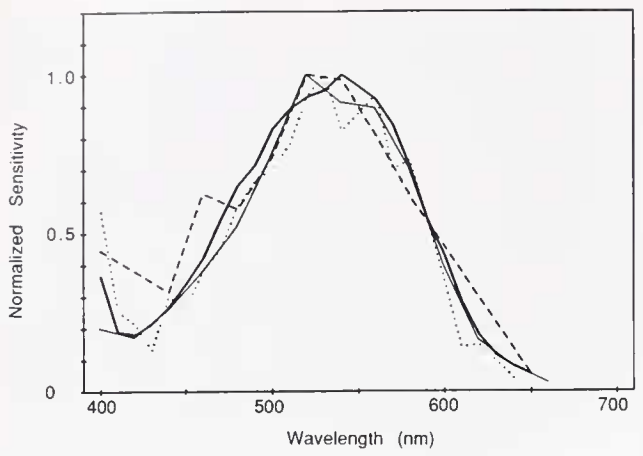

Figure 6. A comparison of the results of the four techniques. Dark solid line: scan technique. Light solid line: criterion technique. Dotted line: interpolation technique. Dashed line: Ramp technique.

Mote, 1982; see also Cronin, 1985; Cronin and Forward, 1988). Most stomatopods also have the 8th cell in all ommatidia (Waterman, 1981; Marshall, 1988), and possess excellent sensitivity to ultraviolet (UV) wavelengths (Schiff, 1963; Cronin, 1989). The presence of UV receptors with sensitivity extending into the spectral range we studied was probably the cause of the large variation of sensitivity we observed at 400 nm.

Stomatopods are brightly colored and display their colors prominently in intraspecific and interspecific communication (Caldwell and Dingle, 1975). In *Gonodaetylus oerstedii*, colors are known to play a role in territorial behavior (Hazlett, 1979). Like many stomatopod species, *G. oerstedii* inhabits shallow, well-lit water, and is active during the daytime (Dominguez and Reaka, 1988). There is every reason to expect that the ability to recognize hue exists in some stomatopods, particularly in the gonodactyloids.

In previous intracellular optical investigations of *G. oerstedii*, evidence has been found that only one long-wavelength spectral mechanism exists in the peripheral retina (Cronin, 1989). In contrast, the tiering of rhabdoms in four of the rows of the central band would be expected to produce up to four dichromatic, long-wavelength mechanisms there (Marshall, 1988). For these reasons, we selected the medial peripheral ocular region for this first study.

Results clearly suggest a single receptor class that responds identically to all four experimental approaches (Fig. 6). This function peaks near 540 nm, has a half bandwidth of 125 nm, and has the typical form of a spectral sensitivity function produced by a single visual pigment.

Does the measured function express the true spectral sensitivity of the photoreceptors of peripheral ommatidia? Several lines of evidence suggest that it does. The intracellular optical response is almost certainly coupled to photopigment absorption, at least at long wavelengths, in numerous species of insects (Stavenga, 1979; Bernard and Stavenga, 1979; Bernard and Wehner, 1980; White *et al.*, 1983; Weyrauther, 1986). Crustacean retinular cells have mobile pigment granules that respond to visual stimulation (Ludolph *et al.*, 1973; Olivo and Chrismer, 1980); it is probably these mobile pigments that bring about the measured reflectance changes (Cronin, 1989). Therefore, the responses we measured almost certainly originate in the visual cells and represent the true visual sensitivity.

The close correspondence of results of the various methods (Fig. 6) indicates that any of the methods may be used in the future. Clearly, the spectral scan technique is the most desirable for general use, since it is not only faster by almost an order of magnitude, but also produces the most accurate spectra. Scanning has also proven superior in electrophysiological work (Franceschini, 1984; Menzel *et al.*, 1986).

While scanning is justified for work with a single receptor mechanism, it may have serious drawbacks when applied to multiple receptor classes within a single eye region. This is because the sequence of wavelengths may affect the separate classes differently. For instance, separate chromatic adaptations of the classes may occur while the scan is in progress, but at different parts of the scanned spectrum. Another, somewhat analogous effect may occur with a single receptor class if the scanning intensity is sufficient to cause photopigment conversion; the ratio of photopigment (rhodopsin) to product (metarhodopsin) would then vary throughout the scan. Such effects are generally revealed by a change in shape of the measured function for scans in different directions. In our work, the spectral shapes measured in both directions were identical, providing no evidence either for multiple receptor classes in the scanned regions or for alterations in the rhodopsin/metarhodopsin mixture content.

It is not always knowable in advance whether spectral scanning is justified for use with the photoreceptors of a particular eye region. In such cases, the criterion technique is the best alternate technique of choice. It is as efficient as the other non-scanning techniques, and can be used to test the response at selected wavelengths for relative sensitivity, or for the changes in response waveform or sensitization that are generally associated with multiple receptor classes (Cronin, 1989).

The overall results suggest that spectral sensitivity in this eye region is conferred by a single, unfiltered rhodopsin. The function peaks smoothly, falls steeply at longer wavelengths, and declines more gradually at shorter ones. However, the bandwidth at half-maximum (125

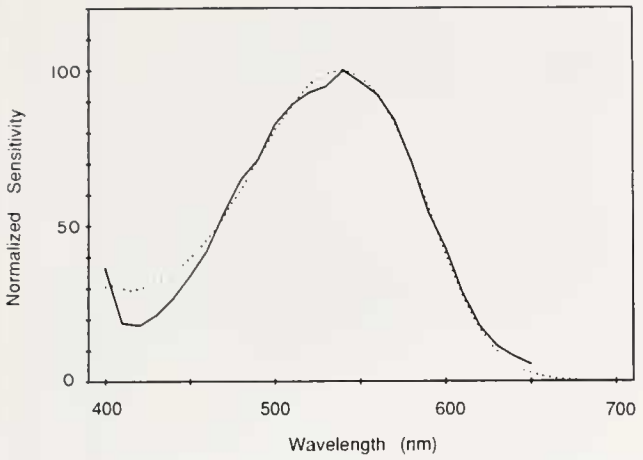

Figure 7. Solid line: average results of spectral scan experiments. Dotted line: computed absorptance spectrum for a rhodopsin having a 537-nm maximum and a peak absorbance of 0.5. The dotted curve is normalized to its maximum, for comparison to the sensitivity function.

nm) is about 25% broader than the 102-nm half bandwidth of the absorption spectrum of a rhodopsin in this spectral location (The absorption spectrum was calculated using an 8th-order polynomial developed by G. D. Bernard and kindly provided by him.) The discrepancy is easily resolved by considering self-screening by the rhodopsin, an effect that broadens the absorption function. In Figure 7 the average curve generated by spectral scanning is plotted together with a computed absorption curve for a rhodopsin peaking at 537 nm and with a maximum density of 0.5. The match between the curves is excellent. In this ocular region, *G. oerstedii* has a sensitivity maximum almost 20 nm to longer wavelengths than that of the squilloid, *Squilla empusa*, which peaks at 520 nm (Trevino and Larimer, 1969).

The techniques described here will now be applied to measure the spectral sensitivities of the various ommatidial rows of the central band. Learning whether the stomatopods possess the diversity of color receptors they seem capable of making will be a demanding, but exciting, task.

Acknowledgments

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